

ON THE STRUCTURE OF THE RESIN-SECRETING GLANDS IN SOME AUSTRALIAN PLANTS.

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(With Text-figures 1-12.)

INTRODUCTION.

While engaged upon an investigation of the resinous secretion of the bud in certain Australian genera of the Natural Orders *Sapindaceae*, *Leguminosae* (Sub-Order *Mimosae*), *Compositae*, *Goodeniaceae* and *Myoporineae*, the writer's attention was drawn to certain types of glandular hair, some of which have not been recorded previously for these Orders.

Since in all cases the developmental stages throw an interesting light upon the structure of the mature gland, and since the results obtained might prove to be of systematic value, it is thought desirable to place these observations on record.

Glandular hairs are described for the following species:—*Dodonaea viscosa* Linn. (*Sapindaceae*), *Acacia rupicola* F. v. M., *A. armata* R. Br., *A. pycnantha* Benth., *A. verniciflua* Cunn., (*Leguminosae*, Sub-Order *Mimosae*), *Lirodeia achillaeoides* R.Br., *Helichrysum semipapposum* DeCand., and *Humea cassiniacea* F. v. M. (*Compositae*), *Myoporum serratum* var. *insulare* R.Br., *Myoporum serratum* var. *viscosum* R.Br., and *Eremophila latifolia* F. v. M. (*Myoporineae*).

My thanks are due to Professor Osborne, University of Adelaide, for the interest he has shown during the progress of the work.

DESCRIPTION OF GLANDULAR HAIRS.

N. O. SAPINDACEAE.

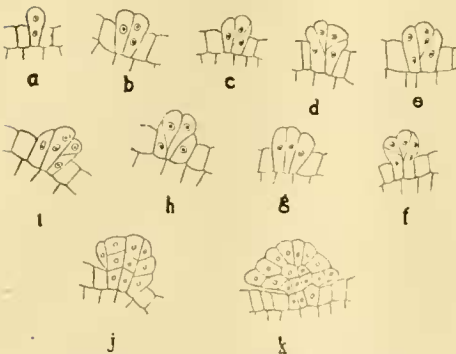
In his account of the *Sapindaceae*, based upon Radlkofer's monograph (2), Solereder states that glandular hairs are widely distributed, and are present on young leaves throughout the order (3, p. 230). The glands are described as being multicellular peltate scales, in which the cells of the shield either show a radial arrangement (*Arytera*), or are polygonal and irregularly placed (*Filicium*, etc.). It is recorded that in some genera, e.g., *Melanodiscus*, the external glands are analogous to glandular shaggy hairs, since they possess a palisade-like secretory region at the periphery.

In *Dodonaea viscosa*, which was examined by the present writer, the glandular hairs resemble the *Melanodiscus* type. They are large in proportion to the thickness of the young leaf, and show a tendency towards radial arrangement of the

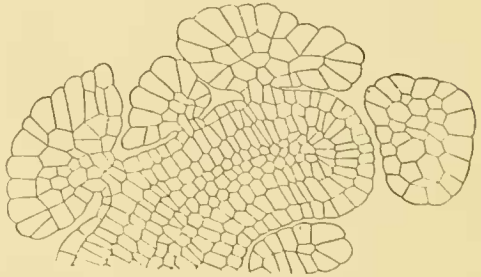
*The observations recorded in this paper were made while the writer held the position of Demonstrator in Botany, The University of Adelaide.

peripheral head-cells. Sometimes this tendency is very marked, giving the gland a colleter-like appearance, while often there is no sign of peripheral elongation, the gland merely being a mass of polygonal cells, irregularly arranged.

Development of the Glands.—The first sign of gland development in *Dodonaea viscosa*, is the projection from the epidermis of a papillose cell which reaches a height of about twice that of the adjacent epidermal cells (Text-fig. 1a). The nucleus divides and the first wall is formed in a vertical direction, dividing the initial cell of the gland into two cells of equal size (Text-fig. 1b). The second division follows in either of the cells thus formed. The wall is either placed in a slightly oblique position, when the resulting cells are unequal in size (Text-fig. 1c) or it may be vertical, when the resulting cells are equal (Text-fig. 1g). Whether the mature gland possesses a pedestal region, made up of two or three rows of cells, depends upon the manner in which this second wall is formed in the young gland. From observations on a number of glands it seems probable that there are never more than two vertical divisions in the first stages of development, while in a number of cases there is only one. The vertical divisions are followed by a series of oblique divisions (Text-fig. 1c-f, h-i), which result in the formation of a projecting cell mass almost spherical in contour (Text-fig. 1j). At this stage there is a marked increase in the size of the cells making up the gland. Those at the periphery tend to elongate in a radial manner, causing the differentiation of the gland into marginal and central regions (Text-fig. 1k). The mature glands are large peltate hairs which overlap one another and spread out to cover a considerable area of the epidermis (Text-fig. 2). The multicellular



Text-fig. 1. —(a-k). Stages in the development of the glandular hairs of *Dodonaea viscosa* Linn. (x 200).



Text-fig. 2.—Mature glands of *Dodonaea viscosa* crowded and overlapping on surface of young leaf. Note their height in comparison with thickness of leaf. (x 120).

head is borne upon a pedestal of 2 or 3 rows of cells which may become more numerous by later divisions. At maturity the radial elongation of the peripheral cells of the gland is often partly and sometimes totally obliterated by a series of irregular divisions which occur during the later stages of development (Text-fig. 2).

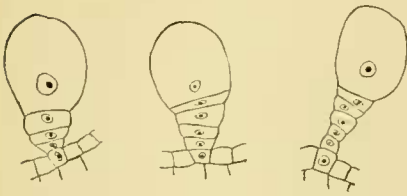
N. O. LEGUMINOSEAE (Sub-order Mimoseae).

Solereder refers to the constant formation of glandular hairs in the *Mimoseae*. The glands may possess a uniseriate stalk of varying length, with a multicellular

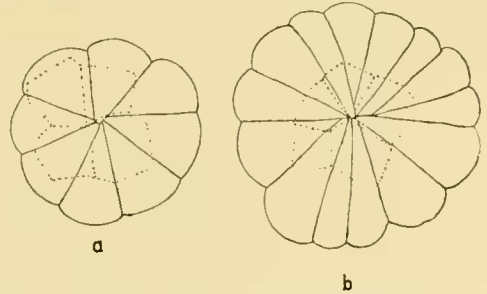
head divided by both horizontal and vertical walls, *e.g.*, certain species of *Parkia*, *Entada*, *Acacia*, and *Albizzia* (3, p. 296), or the head may be shield-like and consist of two layers of cells (certain species of *Mimosa*). Glands with a short stalk and a few head cells have been observed in *Acacia dodonaefolia* Willd., *A. exsudans* Lind., and *A. leprosa* Sieb. (3, p. 296).

In species of *Acacia*, *A. rupicola* F.v.M., *A. verniciflua* Cunn., *A. armata* R.Br., *A. pygmaea* Benth., found in the neighbourhood of Adelaide, the writer observed four distinct types of glandular hair hitherto unrecorded for the genus *Acacia*.

A. rupicola.—In *Acacia rupicola* the mature gland consists of a uniseriate stalk of from three to six small cells surmounted by a large balloon-like head cell (Text-fig. 3). The cells which make up the stalk are not cut off from the base of the head cell, but are formed by a series of parallel transverse divisions within the stalk rudiment. The head cell appears to be more actively secretory than the



Text-fig. 3.—Mature glands of *Acacia rupicola* showing uniseriate stalk of varying length and inflated head cell. (x 230).



Text-fig. 4.—Surface view of glands of *Acacia verniciflua* showing head cells and upper tier of stalk. (x 230).

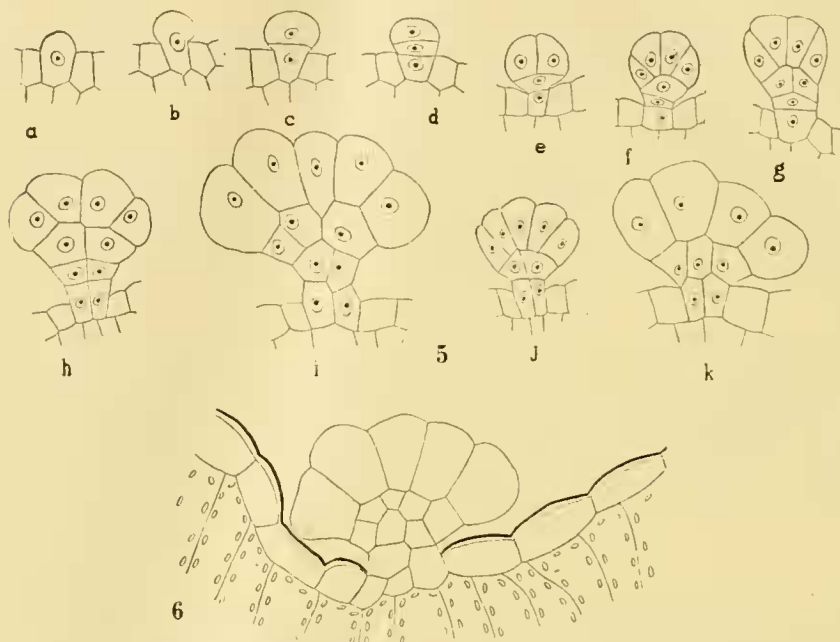
stalk cells. The glands of *A. rupicola* differ from the uniseriate type of gland already recorded for species of *Acacia* by Solereder, in that the head is always unicellular; they probably represent a simpler type of gland than any previously recorded for the *Mimoseae*.

Acacia verniciflua.—In *Acacia verniciflua* the mature gland resembles the type recorded for species of *Mimosa* with shield-like head and consisting of two layers of cells (3, p. 296). Here the normal mature gland is made up of a large head of from eight to sixteen radiating cells in a single layer, supported by a stalk of one or two rows of cells (Text-fig. 4a, b). Each row of the stalk normally consists of four cells, but in some cases irregular divisions may occur, converting the stalk region into a mass of cells of variable number.

Gland Development.

After the first horizontal division differentiating the gland rudiment from the epidermis, a second horizontal division parallel to the first separates the head and stalk rudiments (Text-fig. 5a-d). The third division is vertical in the median plane of the head, and is followed almost immediately by a horizontal division within the stalk, cutting off a second stalk cell (Text-fig. 5e-f). Further vertical divisions are now formed in the head, many of which are quite radial, others nearly so. Closely following the first of these vertical divisions in the head, two vertical divisions

appear bisecting the uppermost stalk cell in planes at right angles (Text-fig. 5g). Similar divisions are then formed in the second stalk cell and ultimately in the basal epidermal cell (Text-fig. 5h). Owing to the position of the original hori-



Text-fig. 5.—(a-h). Stages in the development of the normal gland of *Acacia verniciflua*; *i*, shows commencement of irregular divisions in the upper tier of the stalk; *j*, and *k*, types of gland formed by the omission of the second stalk cell. (x 230).

Text-fig. 6.—Mature gland of *Acacia verniciflua* in which the two-tiered nature of the stalk has been obliterated by irregular divisions during the later stages of development. (x 230).

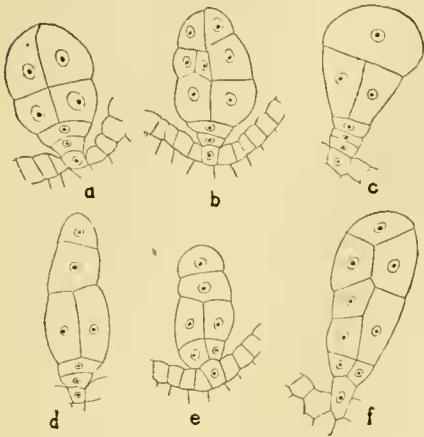
zontal division, at a level sometimes above that of the neighbouring epidermal cells, these basal cells often project for some distance, and appear to form part of the gland (Text-fig. 5h, *i*, *j*).

In Text-fig. 5h we have what is probably the normal type of gland, in which each tier of the stalk is made up of four cells. Text-fig. 5 *j* and *k* represent a type of gland often met where the second stalk cell has been omitted.

With growth of the gland cells, however, an irregular division often takes place in the upper tier of the stalk which is then made up of five or six polygonal cells, irregularly arranged (Text-fig. 5*i*). When this irregular division proceeds to the second tier of the stalk, the resulting gland becomes more complex, the shield-like head being supported by an irregular mass of cells in which all trace of the two-tiered stalk is obliterated (Text-fig. 6).

Acacia armata.—During the development of the glandular hairs in *A. armata* there is marked variation in the sequence and number of cell divisions. This variation is accountable for the number of gland forms which are mingled freely on the surface of the young phyllode. These gland forms resemble one another,

in that the head is always vertically elongated and never shield-like. What appears to be the normal type of gland is figured in Text-fig. 7a. There the head is composed of an octant of cells, and is supported by a short stalk of two cells. The stalk may possess two or three cells (Text-fig. 7a-c), but is often absent



Text-fig. 7.—(a-d). Gland forms of *Acacia armata* in which stalk region is present; e-f, types where stalk is absent. (x 200).



Text-fig. 8.—Glandular hair from the base of the phyllode in *Acacia pycnantha*. (x 200).

(Text-fig. 7e-f). The head in the greater number of glands is characterised by vertical and horizontal divisions which vary in number and sequence (Text-fig. 7b-e). Text-fig. 7f shows a new type of gland which has arisen by the omission of the divisions giving rise to stalk cells.

Acacia pycnantha.—In *A. pycnantha* the glandular hairs are restricted to a zone at the base of the phyllode. The mature glands are elongated in form, and show no differentiation into head and stalk region. They are multicellular, club-shaped bodies in which both vertical and horizontal walls are formed (Text-fig. 8). These glands are of interest in that they resemble the stalkless type of gland found in *A. armata* (Text-fig. 7f), and could conceivably have arisen from this type by the interpolation of further divisions.

N. O. COMPOSITÆ.

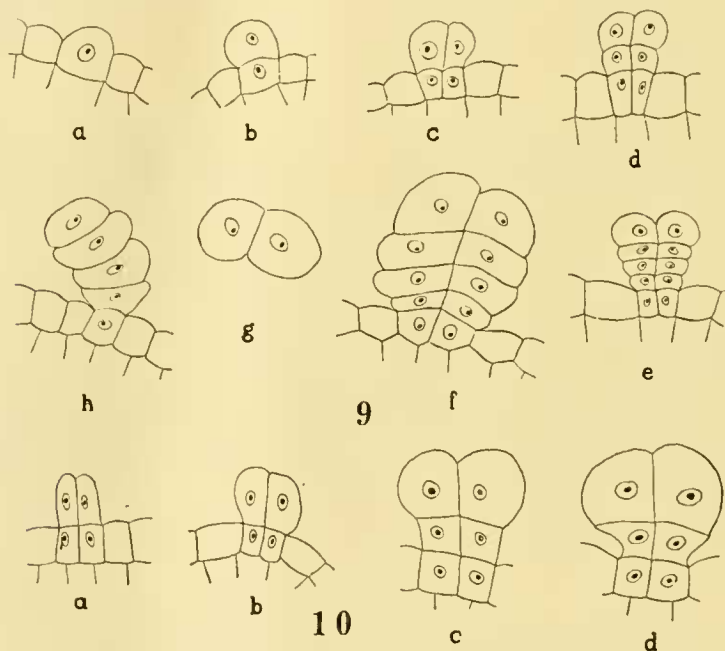
Resin-secreting glandular hairs are widely distributed in the N. O. *Compositæ*, and have been recorded by various investigators (1, 4, 5, 6, 7). The most common type of gland is shortly stalked and possesses a head divided by a median vertical wall into two rows of cells. These are recorded for species of *Anthemis*, *Buecharis*, *Brachylaena*, etc. (3, p. 460), and have been observed by the writer in *Irodea achilleoides* R.Br., *Humea cassiniacca* F. v. M., and *Helichrysum semipapposum* DeCand. The glands figured by Vogl for a species of *Chrysanthemum* (see 3, i., p. 458, fig. 103h, after Vogl), evidently represent a transitional stage between those observed by the writer for *Helichrysum semipapposum* and *Irodea achilleoides*.

Gland Development.—In these three types the first transverse division which cuts off the rudiment of the gland from the epidermis is followed by a median

vertical division in both gland rudiment and basal epidermal cell (Text-figs. 9a-c, 10a-b). This vertical division is followed by a series of transverse divisions parallel to the first transverse wall formed. In the case of *Helichrysium semipapposum* the median vertical division is followed by one transverse division only. The gland cells then increase in size, the upper pair being markedly inflated (Text-fig. 10 c, d). In *Ixodea* and *Humea* there are three transverse divisions following the median vertical division, so that the mature gland possesses two vertical rows, each of four cells surmounting a basal epidermal cell (Text-figs. 9e-f). In the glands of a species of *Chrysanthemum* figured by Solereder after Vogl (3. i., p. 458, fig. 103h.), only two transverse divisions follow the vertical division.

N. O. MYOPORINEAE.

Glandular hairs are of common occurrence in the two genera of *Myoporineae*—*Myoporum* and *Eremophila*. Solereder states that these glandular hairs possess "varied structure within the individual species, but agree in the fact that the



Text-fig.9.—(a-f). Stages in the development of the glandular hairs of *Ixodea achilleoides*; g, h, surface and lateral views of glandular hairs. (x 280).

Text-fig.10.—(a-d). Stages in development of the glandular hairs of *Helichrysium semipapposum*. (x 280).

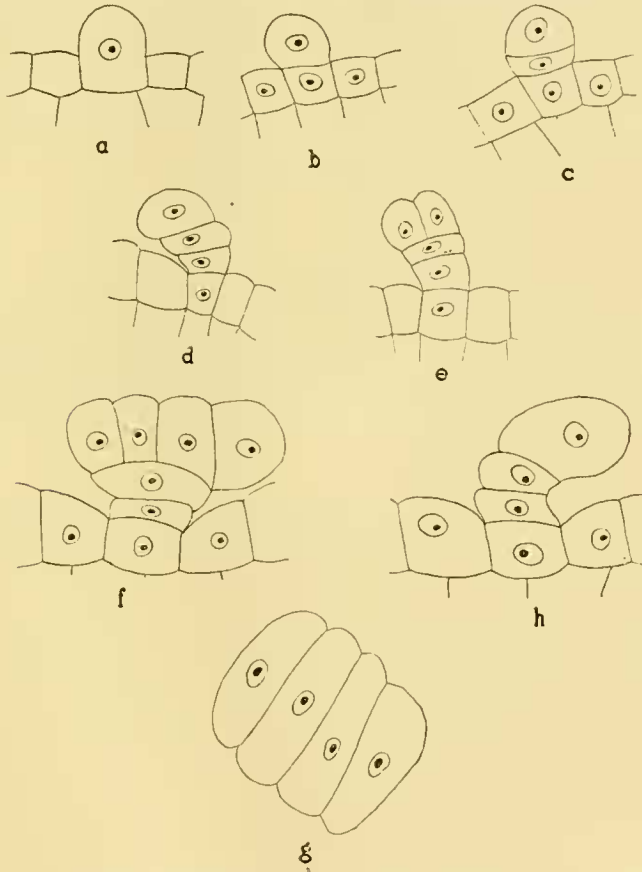
glandular head is, in almost all cases, divided by vertical walls only" (3, p. 626). Glandular and clothing hairs are also known to occur in the same leaf-bud, and, according to Solereder, transitional forms of a dual nature are often found (3, p. 627). These facts suggest that glandular hair formation in the *Myoporineae* is in an unstable condition. Observations made by the writer upon gland develop-

ment in *Myoporum serratum* and *Eremophila latifolia* give additional evidence in support of this view.

The most common type of gland in the *Myoporineae* is that found in species of *Myoporum*, e.g., (*M. serratum* var. *insulare* R.Br., and *M. serratum* var. *viscosum* R.Br.), where a large shield, consisting of four cells in a row, is placed excentrically upon a stalk of two cells.

Gland Development.

Myoporum serratum.—In the initial stages of gland formation a spherical projection from an epidermal cell is cut off from the remaining epidermal cells by a transverse wall (Text-fig. 11a, b). A second transverse division differentiates the gland rudiment into head and stalk regions (Text-fig. 11c). A third transverse division now takes place in the stalk (Text-fig. 11d), and is immediately followed by a vertical division in the median plane of the head (Text-fig. 11e). The 5th and 6th divisions are also vertical in the head, and parallel to the first head division (Text-fig. 11f). Growth of the cells continues after division has ceased.



Text-fig. 11.—(a-f). Stages in the development of the glandular hairs of *Myoporum serratum*; g, h, surface and lateral views of the glands. (x 280).

In the gland head there is greater growth of the cells to one side causing the eccentricity noted above (Text-fig. 11f, h). This unequal lateral growth always occurs in the longitudinal plane of the leaf, and is directed towards the leaf apex. Text-fig. 11g shows gland in surface view.

Eremophila latifolia.—In *Eremophila latifolia* the general plan of gland development resembles that of *Myoporum*. Here, however, the head shield is composed of eight cells and shows two distinct forms within the species.

After the differentiation of the young gland into head and stalk region, the first division which takes place is vertical in the median plane of the head. This is either followed immediately by a horizontal division forming a second stalk cell, or the latter is postponed until the later head divisions have taken place. From the number of glands found in which a head shield with full number of divisions is supported by a single stalk cell, it seems probable that this second stalk division is often omitted. The later divisions in the head are all vertical and according to the arrangement of the walls, give rise to two distinct types of head shield.

In one type the vertical divisions are formed in a radial manner and result in a subspherical shield of 8 radiating cells (Text-fig 12a). In the other type two sets of parallel or almost parallel divisions meet the original, median vertical



Text-fig. 12.—(a-b). Surface view of the two gland forms of *Eremophila latifolia*. (x 230).

division at approximately equal angles, and result in the formation of a shield of eight cells arranged in two rows of four (Text-fig. 12b).

The relation between these types of gland and that of *Myoporum* is obvious. All the gland cells in *Eremophila latifolia* are characterised by the inclusion of a clustered crystal of calcium oxalate.

All text-figures were made at table level, tube at 160 mm., with the aid of Zeiss camera lucida and with Leitz objectives 3 and 6, oculars 2 and 4.

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*The works marked thus were not directly accessible to the writer.